

ENVIRONMENTAL DETERMINANTS OF FLOWERING DATE
IN THE COLUMNAR CACTUS *CARNEGIEA GIGANTEA* IN
THE NORTHERN SONORAN DESERT

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ABSTRACT

Spring flowering of some woody plants in the Sonoran Desert is triggered by the first substantial rain of the cool season. The columnar cactus *Carnegiea gigantea*, as a massive succulent, might be expected to use internal moisture reserves for flower production, thus blooming independently of rainfall. To investigate the environmental signals for flowering in this species, phenological data were collected for 7 to 10 plants from 1967–1988 at Tumamoc Hill, Tucson, Arizona. Climatic and flowering data from 1978–1988 were used to model developmental requirements for the annual peak bloom in May. The models suggested that flowering of *Carnegiea* is controlled by cool-season rain, increasing daylength, and a combination of increasing solar radiation and warming temperatures. A cool-season (November–March) rain of at least 5–9 mm is probably the initial trigger; a post-solstice photoperiod of about 10.5 hr is the second. After days reach 10.5 hours in length, solar thermal units (daily mean temperature \times total daily solar radiation) above a base temperature of 10°C must accumulate to about 489,500 for half the population to flower. Precisely timed seed release is vital to reproductive success in this species. In effect, the rainfall trigger coordinates flowering with soil-moisture availability, and the daylength trigger ensures seed release at the most favorable season for germination.

For most plant species, the timing of flowering and fruiting is an important aspect of reproductive success. In deserts, where germination, emergence, and recruitment are highly episodic (Shreve 1917; Barbour 1968; Sheps 1973; Ackerman 1979; Sherbrooke 1989), the timing of reproduction can be critical. For example, *Fouquieria splendens* Engelm., a drought-deciduous shrub with many wandlike stems, flowers in spring and disperses seeds that germinate during the summer rainy season (Shreve 1917). Unless the summer rains are early and heavy (≥ 25 mm), animals consume the seeds before they can germinate (Bowers 1994). A shift in flowering phenology to a somewhat later bloom might solve this problem, but, as Waser (1979) has demonstrated, the flowering season is tightly constrained by the major pollinators, migratory hummingbirds present only for three to four weeks in March and April. The flowering phenology of *F. splendens* thus reflects a web of climatic and biotic interactions with profound effects on seedling recruitment and eventually on the demography of adult populations. The climatic variable that coordinates these interactions from year to year is the flowering

trigger, in this case the first cool-season storm ≥ 10 mm (Bowers and Dimmitt 1994).

Phenological triggers can be regarded as switches that break bud dormancy and start developmental processes such as leafing and flowering. Once set in motion, these processes advance as a function of temperature, daylength, or some combination of the two (Loomis and Connor 1992). Only three environmental triggers for flowering have been identified: photoperiod, temperature, and moisture (Rathcke and Lacey 1985; Loomis and Connor 1992). Other conditions, such as a particular ratio of soil nutrients, may be prerequisites for normal flower development (Kinet 1993); however, these are not triggers as defined here.

Because rainfall in deserts is temporally and spatially variable, phenological triggers are of particular importance in coordinating flowering, fruiting, and seed dispersal with favorable moisture conditions. The woody Sonoran Desert plants *Larrea tridentata* (DC.) Cov., *Fouquieria splendens*, *Ambrosia deltoidea* (A. Gray) Payne, *Encelia farinosa* A. Gray, and *Acacia constricta* Benth. all flower in response to significant rain, for example (Bowers and Dimmitt 1994). Neither temperature triggers nor photoperiod triggers can accurately coordinate their periods of bloom with periods of greatest soil moisture. Bowers and Dimmitt (1994) suggested that photoperiod is most likely to trigger flowering where the environment is predictable. For example, *Cercidium microphyllum* (Torr.) Rose & Johnston, a small Sonoran Desert tree with photosynthetic bark, blooms once a year during the late spring dry season, one of the few predictable climatic features of the northern Sonoran Desert. Its flowering trigger is apparently a daylength of about 11 hours (Bowers and Dimmitt 1994).

Phenological requirements of most Sonoran Desert plants have not been determined, making it difficult to assess potential feedback mechanisms between flowering phenology and recruitment success. One deterrent has been the lack of a suitable method for the combined analysis of flowering dates and climatic phenomena. Regression or correlation analysis, methods commonly used in arid regions (for example, Sharifi et al. 1983; Nilsen et al. 1987; Turner and Randall 1987; Friedl 1993), may demonstrate which climatic factors are most strongly correlated with flowering, but neither method can identify specific triggers or determine the required developmental heat sums. In this paper, I use a recently developed method (Bowers and Dimmitt 1994) to determine the climatic requirements for flowering in *Carnegiea gigantea* (Engelm.) Britt. & Rose, the giant cactus or saguaro, and to assess the implications of its rather narrow period of bloom. Because *Carnegiea*, like *C. microphyllum*, flowers once a year during the late spring dry season, I expected that its flowering would be cued by daylength also. Moreover, as a columnar

cactus, *Carnegiea* presumably could use internal moisture reserves to produce dry-season flowers, and flowering might therefore be independent of rainfall.

Carnegiea gigantea is conspicuous throughout the Arizona Upland of the Sonoran Desert (Shreve 1951). Mature plants grow to 12 m or more and first bloom at about 2.2 m (approximately 30–35 years of age) (Steenbergh and Lowe 1977). Near Tucson, Arizona, the earliest flowers appear during the last two weeks of April; peak flower occurs during the last week of May through the first week of June (Steenbergh and Lowe 1977). It has long been assumed that daylength and warming temperatures control *Carnegiea* flowering (Johnson 1924; Steenbergh and Lowe 1977); however, the exact phenological requirements have not been studied, and the flowering triggers are unknown. In this study, 10 years of climatic and flowering data from Tumamoc Hill, Tucson, Arizona, were used to derive several models of phenological requirements for *Carnegiea* bloom, including the type of trigger and the heat sum required for flower development. The models that explained the greatest amount of variance in flowering date formed a basis for describing the actual flowering requirements of *Carnegiea*.

METHODS

Study area. Tumamoc Hill, located at 32°13'N, 111°05'W, is a rocky outlier of the Tucson Mountains near Tucson, Arizona. Elevations range from 703 to 948 m above sea level. The rocky, basaltic-andesitic slopes are dominated by *Cercidium microphyllum*, *Encelia farinosa*, *Fouquieria splendens*, *Larrea tridentata*, *Carnegiea gigantea*, *Ambrosia deltoidea*, *Opuntia engelmannii* Salm-Dyck, and other woody perennials characteristic of the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951; Goldberg and Turner 1986). The *Carnegiea* plot is located on a rocky basaltic-andesitic island slightly west of Tumamoc Hill at an elevation of about 703 m.

Daily maximum and minimum temperatures have been recorded at a weather station located about halfway up the hill at the Desert Laboratory (814 m, hereafter referred to as the hill shelter) from 1907 to 1939, 1943 to 1956, and 1976 to the present. From 1932 to 1939, maximum and minimum temperatures were also recorded at the north base of the hill (703 m, hereafter referred to as the base shelter). Between 1978 and 1988, average maximum and minimum January temperatures at the hill shelter were 19.9°C and 7.9°C. In June they were 39.8°C and 24.5°C. The precipitation record extends from 1907 to the present. Rainfall averages 250 mm/year. Almost half falls during July, August, and September; most of the remainder

comes between November and March. Late spring (April to June) and early autumn (October) are typically without rain.

Carnegiea data collection. From 1959 to 1988, a group of *Carnegiea* plants on a 10 m × 10 m plot near the west base of Tumamoc Hill was regularly monitored by staff members of the University of Arizona and the U.S. Geological Survey. The plants were observed weekly from April to October during the period of flowering, fruiting, and active growth. At other seasons, they were generally observed monthly. At each observation, the height of the main stem and of any branches was measured so that growth rates could be determined (Hastings 1961). From 1967 to 1988 (except in 1974 and 1975), the presence of flower buds and flowers on main stems and branches was noted. From 1975 to 1988, the presence of fruits was also recorded. In 1967, the group consisted of 11 plants, 7 of them reproductively mature. In 1984, one of the original 11 died. By 1986, 9 of the 10 remaining plants were old enough to flower, and, in 1988, all 10 flowered.

For 17 of the 22 years from 1967–1988, there was enough information to determine average first and last date of flower, average duration of bloom (the number of days between first and last flower), and the first date when at least half the reproductive plants were in bloom (average flower date). For all but one of the years between 1975 and 1988, it was possible to determine the average first and last dates of fruit, average duration of fruit (the number of days between first and last fruit), and average length of reproductive season (the number of days from first flower to last fruit).

Climate data. No temperatures were available for the *Carnegiea* plot, but, based on elevation, it was assumed that *Carnegiea* plot temperatures would be close to those at the base shelter, which was in operation from 1932–1939. A regression of base versus hill temperatures was used to generate a record of estimated maximum and minimum temperatures for the *Carnegiea* plot for 1978 to 1988. The months used in the regression analysis were January–May 1934. The regression equation for minimum temperature was $y = 0.909x - 2.918$, where y = base shelter temperature and x = hill shelter temperature ($R^2 = 0.845$, $P < 0.001$). For maximum temperature, the equation was $y = 0.927x + 2.809$ ($R^2 = 0.986$, $P < 0.001$).

Determining the heat sum. Phenological analysis is necessarily empirical (Loomis and Connor 1992) and involves comparing the date of flower in a series of years with climatic conditions in each year. Although for most species the date of flower will vary from one year to the next, the accumulated heat, or heat sum, required for flowering should be about the same in every year.

One measure of accumulated heat, often expressed in degree days,

can be defined as the sum of mean daily temperatures above an appropriate base temperature. The summation starts with the date of trigger and ends with the date of flower. The heat sum can be calculated as

$$T_s = \sum (T_d - T_b) \quad \text{if } (T_d - T_b) > 0,$$

where T_s is degree days, T_d is the mean daily temperature, and T_b is the mean daily temperature above a base temperature (a minimum temperature required for growth).

A second measure of accumulated heat, solar thermal units, is a product of daily total solar radiation in langleys and daily mean temperature above a given base (Caprio 1973). Because CO_2 uptake in many cacti increases with daily total solar radiation (Gibson and Nobel 1986; Nobel 1988), it seemed possible that solar thermal units might be a more appropriate measure of heat requirements for saguaro bloom than degree days. Solar thermal units, which can be expressed as langley-degree days, can be calculated as

$$L_s = \sum [(L_d)(T_d - T_b)] \quad \text{if } (T_d - T_b) > 0,$$

where L_s is langley-degree days and L_d is daily total hemispheric solar radiation on a horizontal surface in langleys (Caprio 1973). The University of Arizona, 6 km east of Tumamoc Hill, was the closest station for daily total solar radiation.

When neither the heat requirements nor the date of trigger are known, as was the case for *Carnegiea*, it is necessary to select a range of appropriate trigger dates, then calculate the heat sum between each potential trigger date and the flower date for all years of record (Bowers and Dimmitt 1994). Valid triggers should produce heat sums that converge toward the same value year after year, whereas spurious triggers should produce values that vary greatly from one year to the next. My process of trigger selection is discussed in detail below.

Determining the base temperature. When the base temperature for growth is not known, the heat-sum calculations are made for each trigger date using several potential base temperatures (Arnold 1959). The temperatures used in this study (0, 5, 10, and 15°C) span the range of temperatures at which plants of warm-temperate or subtropical affinities are likely to grow (Hutchinson et al. 1992). The heat sums above a given base were averaged for the years of interest. The base temperature giving the smallest coefficient of variation is considered to be the most likely threshold (Arnold 1959), and the average heat sum above that base represents the amount of heat required for flower development. For this study, heat sums were calculated in both degree-days and langley degree-days.

Determining the dates of flower. In any year, the duration of flower within a population can be several days or weeks. For phenological analysis, it is necessary to select from this time span a single flower date. One common criterion is the first date in each year when half the population is in bloom (Loomis and Connor 1992), referred to here as the average flower date. A preliminary analysis of the *Carnegiea* plot data suggested that the number of plants in the sample was too small to provide a reliable average flower date. Because the apices of the several branches and main stem are typically at different heights above the ground, they experience somewhat different temperature regimes and do not necessarily flower simultaneously. Therefore, instead of the total number of plants (10–11 from 1978–1988), the total number of stems (17–18 from 1978–1988) was used in this analysis. The average flower date then became the first observation date in each year when 50% of the stems were in flower. This changed the flower date in three years: from May 26 to May 19 in 1978, from May 19 to May 27 in 1980, and from May 15 to May 21 in 1987. The average flower date for the ten-year period was the same in either case. The data from 1986 were dropped from the analysis because fewer than half the plants were in bloom on any observation date. Many blackened flower buds were observed, which suggests that a plant pathogen might have been involved.

Determining the phenological triggers. Because the trigger for *Carnegiea* bloom was not known, rainfall, photoperiod, and temperature were considered as potential triggers.

Rains probably act as a flower trigger by raising soil moisture to some threshold value, at which point, given suitable temperatures, flowering processes are initiated. Rainfall amounts are simply useful proxies for soil moisture measurements, which usually are not available. The smallest effective rainfall trigger known for Sonoran Desert shrubs is 9 mm (Bowers and Dimmitt 1994). In the northern Sonoran Desert, rain-triggered plants that flower in spring typically do so in response to the first substantial storm of the cool season (November–March) (Bowers and Dimmitt 1994). These early cool-season rains are an effective means of breaking dormancy, which in some species can be induced by the hot, rainless days of late September and October (for example, *Encelia farinosa* [Ehleringer 1982] and *Grayia spinosa* (Hook.) Moc. [Ackerman et al. 1980]). For this analysis, all cool-season rains ≥ 5 mm were treated as potential triggers for *Carnegiea* bloom. (Lack of October rainfall in 1979, 1981, and 1982 made it seem unlikely that autumn rains are triggers.) When rain fell on several consecutive days, the cumulative total was used as the trigger amount. When two or more different rain events seemed equally likely to have triggered a given flowering

event, heat sums were calculated above the four base temperatures for each one, then the rainfall trigger and base temperature that produced the smallest coefficient of variation were selected.

The following dates were used as potential daylength triggers: October 11 (11.5 hours of daylight), October 27 (11 hours), November 14 (10.5 hours), January 1 (10 hours), January 28 (10.5 hours), February 15 (11 hours), March 1 (11.5 hours), March 17 (12 hours), and March 31 (12.5 hours). This range of daylengths spans the decreasing photoperiods of late autumn and early winter and the increasing photoperiods of late winter and spring.

In cold-temperate climates, where spring warming brings many plants out of winter dormancy, temperature can be an effective means of cuing flower development to climatic trends (vernalization) (Caprio 1973). In the warm-temperate Sonoran Desert, where many winter days are warm enough for plant growth, no plants have been reported to require vernalization. Between November and March, minimum temperatures may range from 0 to 10°C over the course of a single week, and daily maxima as high as 25°C are not uncommon. Given this wide range of daily temperatures in winter and spring and the absence of a prolonged period of winter cold, it seemed unlikely that flowering in *Carnegiea* is triggered by a particular temperature threshold, therefore potential temperature triggers were not analyzed in this study.

Determining flowering requirements. Two types of models for formulating phenological requirements were derived, one type based on rainfall triggers, the other on photoperiod triggers. Climatic and flowering data from 1978–1988 were used to determine the base temperature and required heat sum (in degree days and langley-degree days) as described above. (These 10 years were those for which complete weather records existed.) As noted above, flowering was poor in 1986, and the data for that year were omitted from the analysis.

For each type of trigger and each type of heat sum considered, the best model solution was defined as the one that produced the lowest coefficient of variation. This produced four models, two using degree days, two using langley-degree days. The fit of these models was evaluated with linear regression, using the Julian flower date or the development period as the dependent variable. The development period was defined as the number of days from the date of trigger to the date of flower. The independent variables were: 1) degree days during the development period (rain trigger), 2) degree days per day during the development period (rain trigger), 3) degree days during the development period (photoperiod trigger), 4) degree days per day during the development period (photoperiod trigger), 5) Julian date of the degree-day rain trigger, 6) langley-degree days

during the development period (rain trigger), 7) langley-degree days per day during the development period (rain trigger), 8) langley-degree days during the development period (photoperiod trigger), 9) langley-degree days per day during the development period (photoperiod trigger), 10) langley degree-days from rain trigger to photoperiod trigger, and 11) Julian date of the langley-degree-day rain trigger.

RESULTS

Carnegiea flowering dates. From 1968–1988, the date of average flower, that is, the first date when at least 50% of reproductive plants were in bloom, occurred as early as April 25 and as late as June 1. The mean was May 19 (SE = 1.84). One plant produced flowers and fruits in May 1986, then twice initiated flower buds, which aborted, in August of the same year. First flower occurred as early as April 18, last flower as late as June 20. The average date of first flower was May 8 (SE = 1.70). June 12 was the average date of last flower (SE = 1.66). Duration of bloom averaged 36 days (SE = 2.33).

Carnegiea fruiting dates. The dates of first and last appearance of fruit were May 27 (SE = 2.15) and July 1 (SE = 1.74). Fruit duration averaged 41 days (SE = 1.85). The reproductive season from first flower to last fruit averaged 64 days (SE = 2.54).

Flowering requirements. Of the many model solutions considered, the best were: 1) first cool-season rain ≥ 5 mm, heat sum = 546,944 langley-degree days above 10°C (CV = 0.056); 2) daylength = 10.5 hr (January 28), heat sum = 489,460 langley-degree days above 10°C (CV = 0.062); 3) first cool-season rain ≥ 9 mm, heat sum = 1039 degree days above 10°C (CV = 0.057); and 4) daylength = 10.5 hr (January 28), heat sum = 1995 degree days above 0°C (CV = 0.050) (Fig. 1a, b).

In the linear-regression analysis, several independent variables explained a significant proportion of the variance in flower date: degree days/day from the rain trigger to the flower date ($R^2 = 0.869$, $P < 0.001$), langley-degree days/day from the rain trigger to the flower date ($R^2 = 0.900$, $P < 0.001$), langley-degree days from the photoperiod trigger to the flower date ($R^2 = 0.70$, $P < 0.006$), and degree days from the photoperiod trigger to the flower date ($R^2 = 0.50$, $P < 0.03$) (Table 1). No matter which dependent variable was used (flower date or length of the development period), langley-degree days explained a higher proportion of the variance than degree days, and therefore seems a more suitable unit for determining heat sums.

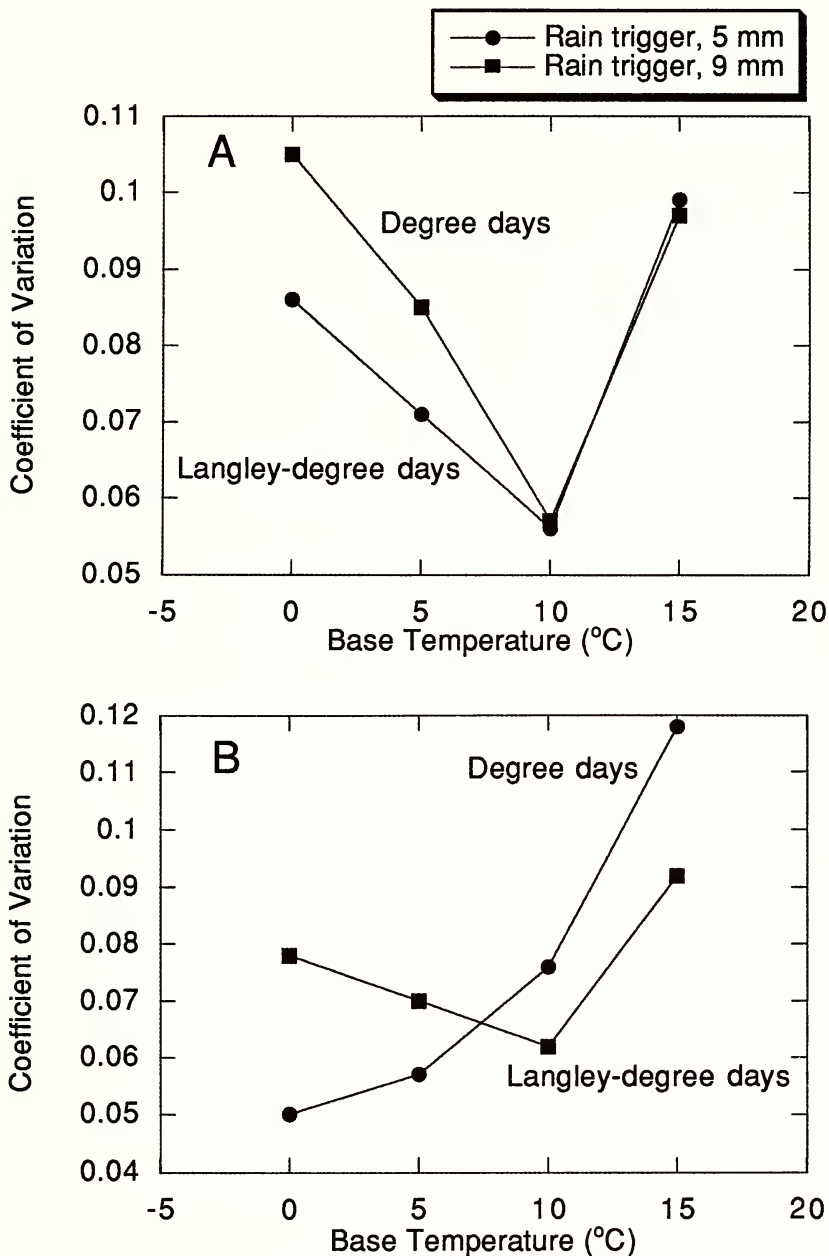


FIG. 1a. Relationship between base temperature and the coefficient of variation for average flower of *Carnegiea gigantea* from 1978–1988 using heat sums calculated from rainfall trigger to date of flower.

FIG. 1b. Relationship between base temperature and the coefficient of variation for average flower of *Carnegiea gigantea* from 1978–1988 using heat sums calculated from photoperiod trigger to date of flower.

TABLE 1. R^2 VALUES FROM THE LINEAR REGRESSIONS OF *CARNEGIEA* FLOWER DATE VERSUS 7 CLIMATIC VARIABLES. All dates were converted to ordinal numbers. DD = degree days (for base temperature, see text), DD/D = degree days/day, LDD = langley-degree days, LDD/D = langley-degree days/day, RTD = rain trigger date, PTD = photoperiod trigger date (10.5 hours after winter solstice), FD = flower date.

Independent variable	Dependent variable	R^2	P
Degree-day models			
DD from RTD to FD	Flower date	0.004	0.862
DD from PTD to FD	Flower date	0.504	0.022
RTD	Flower date	0.074	0.447
DD/D from RTD to FD	Days from RTD to FD	0.869	0.000
DD/D from PTD to FD	Days from PTD to FD	0.191	0.207
Langley-degree day models			
LDD from RTD to FD	Flower date	0.203	0.223
LDD from PTD to FD	Flower date	0.698	0.005
LDD from RTD to PTD	Flower date	0.113	0.377
RTD	Flower date	0.130	0.340
LDD/D from RTD to FD	Days from RTD to FD	0.900	0.000
LDD/D from PTD to FD	Days from PTD to FD	0.009	0.805

DISCUSSION

On the basis of the model solutions, it appears that flowering in this species is a complex phenomenon involving several different climatic signals. The model that uses a rain trigger and the average daily temperature sum (langley-degree days/day) explains 90% of the variance in length of the development period (Table 1). This model produces a strong inverse correlation between the length of the development period and the average daily heat sum (Fig. 2). This is not surprising; if the model works, a short development period would necessarily be correlated with higher daily temperature values, because there would be fewer days in which to achieve the required temperature sum. Put another way, warmer days speed cell development, thus producing shorter development periods. It appears virtually certain, therefore, that rainfall is involved in triggering *Carnegiea* bloom.

Other evidence supports this hypothesis, as well. The two best rain-trigger models produced strongly V-shaped curves and, at a base temperature of 10°C, low coefficients of variation (Fig. 1a). These traits are apparently typical of rain-triggered perennials in the Sonoran Desert, e.g., *Larrea tridentata* and *Encelia farinosa* (Bowers and Dimmitt 1994). The salient characteristic of a valid trigger is the strong convergence from year to year on a single heat sum (Bowers and Dimmitt 1994). Among the many potential rain triggers for *Carnegiea* bloom, all but two produced linear, rather than V-shaped, curves and comparatively large coefficients of variation; in short, they failed to converge on a single heat sum. It appears, there-

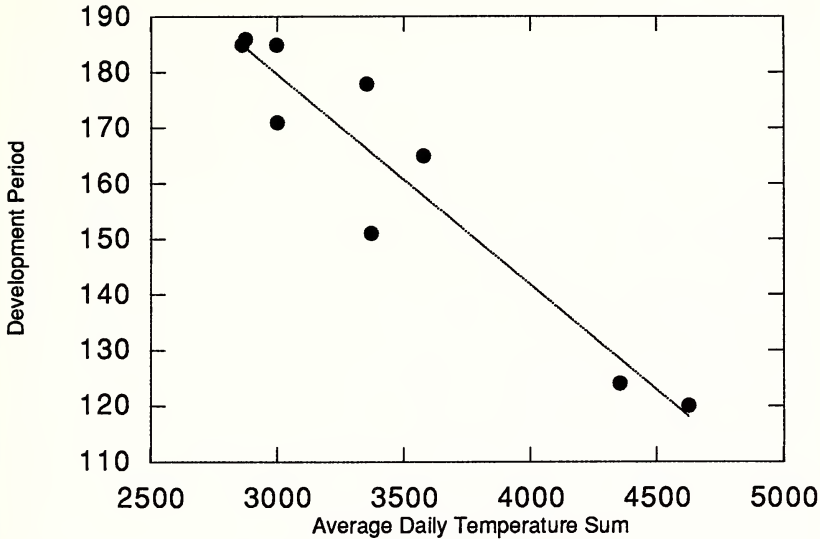


FIG. 2. Length of the development period in days as a function of the average daily temperature sum in langley-degree days above 10°C. The development period extends from rainfall trigger to date of flower.

fore, that most of the potential rain triggers examined in this study had no bearing on *Carnegieia* bloom. Two, however, the first cool-season rains ≥ 5 mm and ≥ 9 mm, stood out from the rest, making it seem very likely that cool-season rain plays a vital role in triggering *Carnegieia* bloom.

The photoperiod/langley-degree day model accounts for almost 70% of the variance in flower date, strongly suggesting that photoperiod is also involved in the timing of *Carnegieia* bloom. If this high correlation were due solely to the mechanical interaction between temperature and time, such that the highest temperature sums were accumulated during the longest periods of time, one would expect a strong positive correlation between langley-degree days/day and length of the development period. This does *not* occur, however (Fig. 3), indirectly supporting the idea that photoperiod does indeed play a role in *Carnegieia* flower development.

Carnegieia plants apparently integrate the two triggers and the required heat sum in a complex way. The rainfall trigger might make the plant apex "competent" (McDaniel 1994). In the case of *Carnegieia*, the initial trigger may be a rain of at least 5–9 mm. Competence, sometimes referred to as "floral induction" (McDaniel 1994), occurs when leaves undergo physiological changes that make them capable of responding to a trigger that stimulates floral initiation (Kinet 1993), also called "floral evocation" (McDaniel 1994).

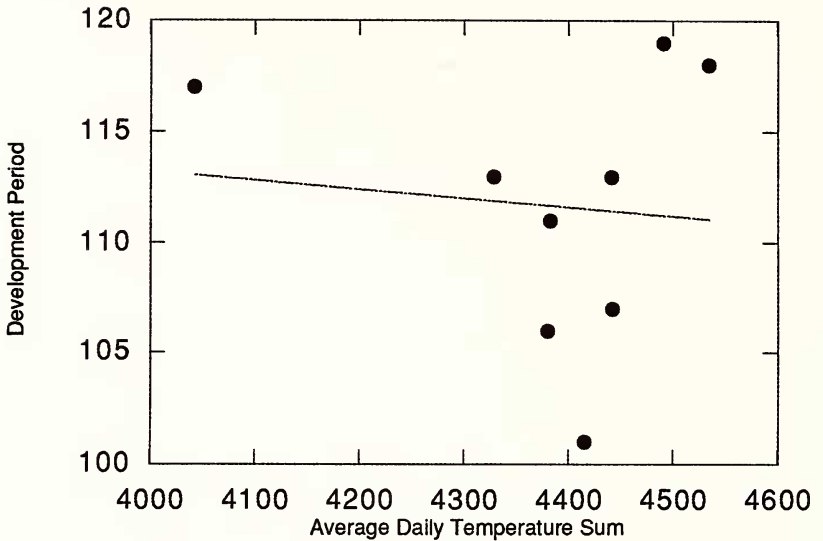


FIG. 3. Length of the development period in days as a function of the average daily temperature sum in langley-degree days above 10°C. The development period extends from photoperiod trigger to date of flower.

In *Carnegiea*, the trigger for floral evocation might be the 10.5-hour photoperiod. At the floral-evocation stage, meristematic cells at the plant apex are committed to flower production (Kinet 1993; McDaniel 1994). Further flower development then occurs as a function of warming days and increasing solar radiation. For *Carnegiea*, roughly 489,500 langley-degree days above 10°C are required for half the population to bloom.

Whether this verbal model accurately describes flower development in *Carnegiea* is not known. The physiological processes and anatomical stages involved are best studied in a laboratory setting. This model identifies environmental factors that could be the focus of experimental work.

Dual flowering triggers are known for other species. Opler et al. (1976) suggested that in the lowland tropical dry forest of Costa Rica, flower induction is triggered by short days and that further flower development is triggered by the first rain of 25 mm. Many crop species, including winter wheat and winter barley, have both vernalization and photoperiod requirements (Loomis and Conner 1992; Kinet 1993).

Daylength is known to trigger flowering in other cacti, including *Schlumbergera truncata* (Haw.) Moran, and also affects flower production and stem tip growth (Nobel 1989). In *Carnegiea*, the existence of a photoperiod requirement is indirectly confirmed by the

fact that the plants flower only once a year despite substantial late summer storms in most years. Rainfall is also known to trigger flowering in cacti; the small cactus *Mammillaria microcarpa* Engelm. can flower as many as three times a year, always after a substantial storm (Mark A. Dimmitt unpublished data). Certain indirect evidence also points to the importance of rainfall as a flowering trigger in *Carnegiea*. In a marginal population in southeastern California, only 8% of plants of reproductive age flowered after a very dry winter (Brum 1973). All the flowering plants grew in washes where they presumably harvested more water than nonflowering plants on adjacent flats (Brum 1973).

I had anticipated that *Carnegiea*, as a succulent plant with a large volume: surface area ratio, would flower independently of rainfall. This is apparently not the case. Stored water alone might not be sufficient to initiate flowering in this species. The flowering requirements emphasize the extent to which even a massive cactus like *Carnegiea* apparently depends on rainfall of the current growing season. As for other rain-triggered species in the northern Sonoran Desert, the requirement for substantial cool-season rain apparently coordinates floral induction with soil moisture and perhaps prevents flowering in extremely dry years.

One effect of the daylength trigger is to ensure that the plants do not flower at a time of year when their reproductive effort would almost certainly be wasted. A number of circumstances combine to make this seem a likely hypothesis. *Carnegiea* disperses its seeds in late spring and early summer, germinates only during the summer rainy season, and has limited seed viability (Steenbergh and Lowe 1977). The fallen seeds are rapidly consumed by a variety of granivores (Steenbergh and Lowe 1977). *Carnegiea* circumvents these hazards to some extent by dispersing seeds immediately before or with the onset of summer rains. Virtually all germination that occurs in the wild happens within the first few weeks after seed dispersal (Steenbergh and Lowe 1977). Based on 67 years of record, Greene (1963) stated that a reasonable approximation for average onset of summer rains at Tucson is July 2; the *Carnegiea* flowering record on Tumamoc Hill shows that the average date of last fruit is July 1. The date of last fruit varies little from year to year (a standard deviation of only 6 days). Clearly, one effect of the daylength trigger is to restrict flowering, and therefore seed dispersal, to the season when reproductive success is most likely.

As the flowering record at Tumamoc Hill shows, the date when half the *Carnegiea* population is in bloom can vary considerably from year to year, despite the invariability of the photoperiod trigger. This is because flowering is earlier in a warm year, when the required heat sum is achieved fairly quickly, and later in a cool year, when solar thermal units accumulate more slowly. Variation in flow-

ering time also occurs across the range of the species. In a given year, the plants flower earlier at lower latitudes (Steenbergh and Lowe 1977), largely because the lower elevations result in milder winters, and solar thermal units therefore accumulate more rapidly. As noted above, within-year variation may occur at a given locality, as well. In the Tucson area, rare individuals have been observed in bloom in August (Elizabeth A. Pierson personal communication), September, October, December, and January (Steenbergh and Lowe 1977). Triggers for these aberrant individuals are not known. Some apparently never flower in spring (Raymond M. Turner personal communication), and these may possess genetic variation in their daylength triggers. Individuals that flower outside the normal blooming period rarely if ever produce offspring (Steenbergh and Lowe 1977).

The relatively brief duration of *Carnegiea* bloom (an average of 36 days) contrasts with the long flowering periods of some other columnar cacti in the northern Sonoran Desert, particularly *Stenocereus thurberi* (Engelm.) Buxb., which flowers from April to July, and *Lophocereus schottii* (Engelm.) Britt. and Rose, which flowers from April to August (Wiggins 1964). Kochmer and Handel (1986) pointed out that selective pressure exerted by pollinators generally does not push flowering times beyond the boundaries imposed by phylogenetic constraints. Because the flowering of *Carnegiea* in April and May occupies only a small portion of the lengthy flowering season available to columnar cacti as a group, it seems possible that some factor other than (or in addition to) phylogeny has determined its flowering time. Likely selective factors include competition for pollinators, pollinator availability, and seed germination needs (Rathcke and Lacey 1985). At present, insufficient data are available to decide which if any of these factors have exerted selective pressure on flowering time of *Carnegiea*.

The annual flowering of *Carnegiea* reflects a network of climatic and biotic interactions. Clearly, properly timed seed release is vital to reproductive success in this species. Because *Carnegiea* seeds are short-lived and avidly consumed, few if any survive past the summer rainy season. Early and heavy rains are therefore crucial for seedling emergence, and, just as important, seeds must not be released too early or too late. The timing of the first substantial winter storms varies greatly from year to year. Such a variable phenomenon could produce a broad range of potential flower dates and thus lengthen the period of seed dispersal. Because it does not vary from year to year, a photoperiod trigger might restrict the period of bloom to a much narrower window. In effect, the photoperiod trigger ensures that the seeds will be dispersed in time for germination during the summer rains.

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